THE AMPULLÆ OF LORENZINI IN ACANTHIAS VULGARIS*

By H. E. Metcalf

Introduction

In the past thirty years a considerable amount of work has been done on the lateral line system in the Selachians, in connection with which the ampullæ of Lorenzini have been described. These ampullæ occur in the Selachians only, and for that reason are important, as other Ichthyopsida have lateral line systems which show no traces of these ampullæ. In the Selachians the ampullæ have almost invariably been classed with the lateral line system. There is a great difference of opinion among investigators as to the exact function of these structures; whether they merely do the same work as the lateral line system, or whether they have a special function which is lacking in the rest of the lateral line system. These differences of opinion were not confined to the ampullæ alone, but the lateral line system itself was a basis of dispute. The lateral line system was at first held to be purely secretory, but later was believed to have sensory as well as secretory functions. This opinion is at present generally accepted, but the exact function of the ampullæ is still in doubt, and there are many conflicting statements regarding them.

According to all authors these organs were first described by Stephan Lorenzini in 1678. Since that time many papers have dealt with the subject, most of them treating the ampullæ only superficially, being good for the location of the organs only. Leydig (52), and Boll (68) said that these ampullæ should be classed with the lateral line system. They also saw in them structures which led them to say that the ampullæ were homologous with the electric organs of the torpedo. But the discovery of ampullæ in that fish soon disproved that theory. In 1852 Jacobson had said that the

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lateral line system was sensory in function, and that the ampullæ belonged in the same category. Later upon a closer examination of the organs he admitted that the old hypothesis of a secretory function was correct, and that, as the ampullæ were so closely related to that system, they also were secretory in function.

In 1852, both Leydig and Müller published their works on the anatomy of the Selachians, in which they ascribed a secretory function to the ampullæ. This hypothesis was supported by a new work of Leydig in 1868. Considering the technical and optical methods of the time, the results of these two men were truly remarkable, and for a period of nearly thirty years little or nothing was added to the subject; while the belief that the ampullæ were secretory prevailed.

Boll in 1868, and Todaro in 1870 were responsible for the name of Lorenzini'sche Ampulle as applied to these organs.

The histological structure has never been thoroughly worked out, except by Forsell (98) who was not certain of his results, because only material preserved in formalin was available for his use. His paper has an excellent review of all the literature on the subject up to 1897. Peabody (97) published a short article on the innervation of these ampullæ as shown by means of methylin blue preparations. None of the workers have found mucus cells in the epithelium of the ampullæ, and only Parker (10) has done anything in the way of experimental evidence as to their function.

The ampullæ in Acanthias vulgaris are arranged in eight definate groups; two on the dorsal surface (Fig. 1), four on the ventral (Fig. 2), and two on the lateral surfaces. (Fig. 3-A). As might be expected, these groups are bilaterally symmetrical. The position of six of these groups is approximately visible in an external view of the snout, as the openings of the ducts give an indication of the internal arrangement of the organs. Thus on the dorsal side of the snout are a pair of triangular groups of openings. Dissection shows these to be connected with a pair of triangular groups of ampullæ (Fig. 1-A), these groups being smaller in extent than the area occupied by the external openings. From these ampullæ the ducts radiate in all directions, except toward the ventral surface.

On the ventral surface of the snout, in front of the mouth, the openings of the ampullæ are evenly distributed over the entire ventral surface. (Fig. 2). On dissecting away the skin, however, it is seen that the three cartilege bars of the rostrum, which run almost straight forward, divide the ampullæ into four rectangular groups. (Fig. 2—1, 2, 3, 4.) Here as in the dorsal surface the duct run in all directions, forward, laterally, back and ventrally,

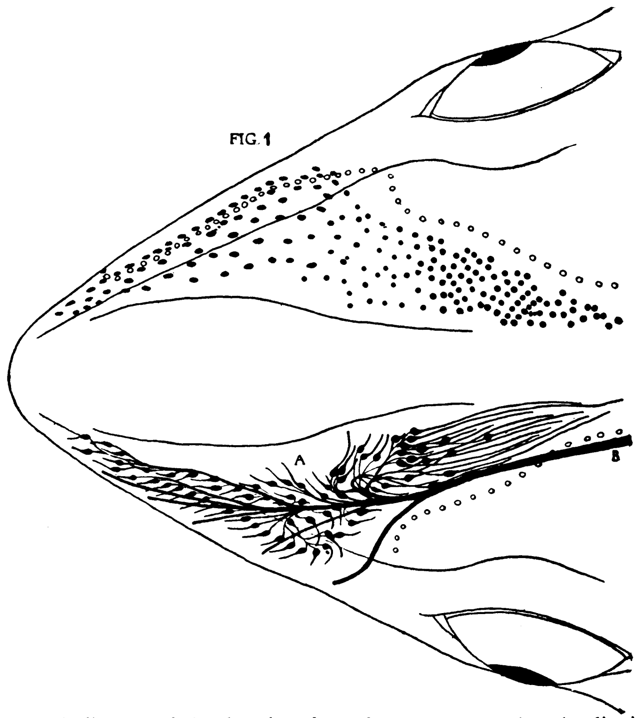

Fig. 1. A diagram of the dorsal surface of the snout showing the distribution of the openings on the right, and the approximate location of the ampullæ on the left. About natural size.

with the posterior ampullæ of the two lateral groups running posteriorly to open at the extreme corners of the mouth. (Fig. 2-B).

On the side of the head, posterior to the mouth, and between the eye and the first gill slit, occur the spiracular ampullæ (Fig. 4-A), all of which have long canals. These open at the posterior

region of the mouth, and in the line of openings just anterior to the first gill slit.

The two groups on the dorsal surface of the snout are innervated by the opthalmicus superficialis (Fig. 1-B), those of the ventral groups by the buccalis (Fig. 2-C), and those of the spiracular region by the mandibularis externus (Fig. 4-B) branches of the seventh, or facial nerve. These branches also innervate the lateral line system in those regions.

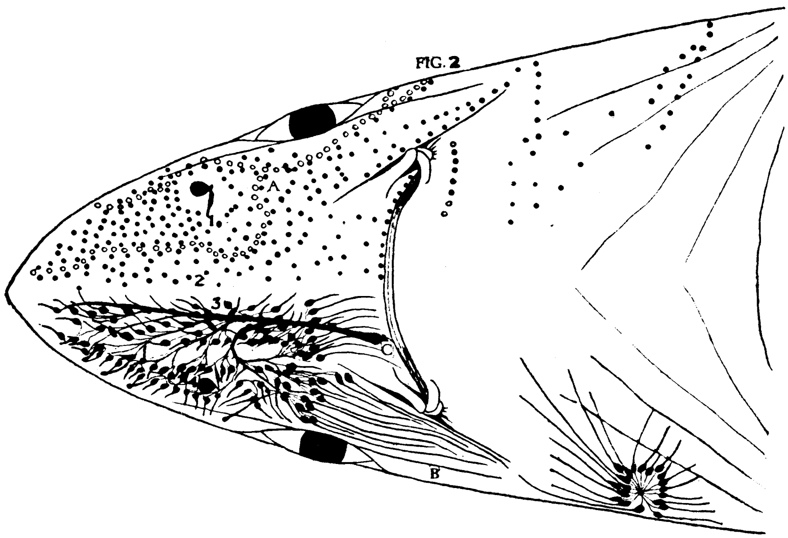

Fig. 2. A diagram of the ventral surface of the snout showing the distribution of the openings on the right, and the approximate location of the ampullæ on the left. About natural size.

The number of ampullæ is not constant, there being from 1,200 to 1,900 in each adult fish. The number in the late stages of the "pup" is approximately the same, so that there is no addition to the number after the fish is born. There are about 500 dorsal ampullæ, 900 ventral and anterior to the mouth, and 200 lateral and ventral, posterior to the mouth. There are no ampullæ posterior to the first gill slit.

All of the ampullæ have definate positions in the head, and in each group the ducts run forward, laterally and backwards as well

as in all intermediate directions. Some of them also point up, and some down, so that there are ducts radiating in all directions, giv-

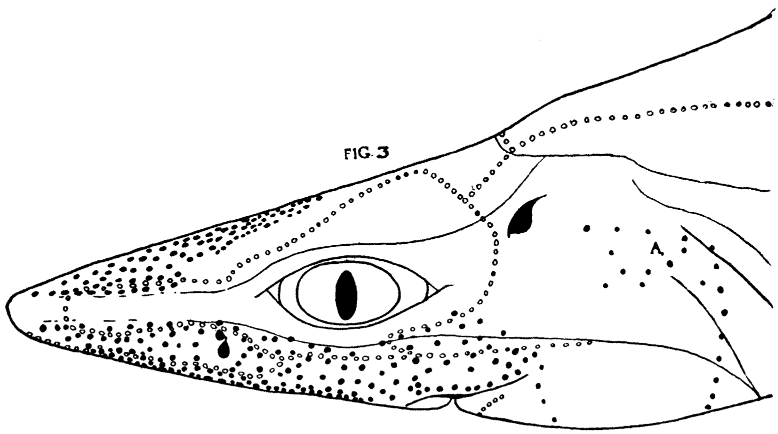

Fig. 3. A diagram of the lateral surface of the snout showing the distribution of the openings. About natural size.

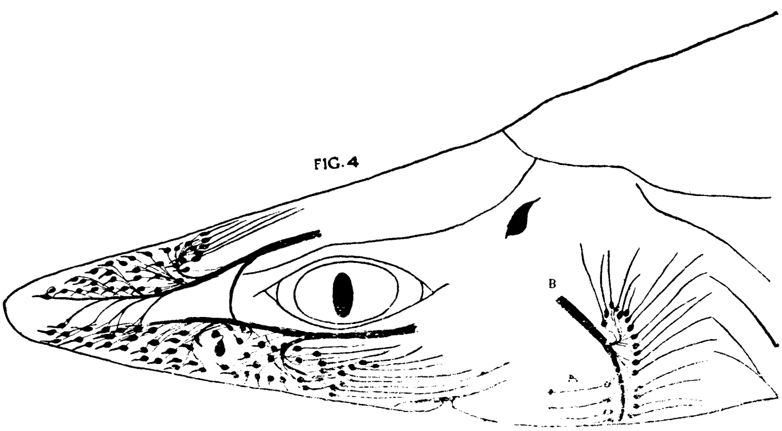

Fig. 4. A diagram of the lateral surface of the snout showing the approximate location of the ampullæ. About natural size.

ing a chance for the reception of a stimulus from any side, above or below. This will be referred to later in discussing the exact function of the ampullæ.

This problem of their function is an interesting one. They are full of mucus, yet no mucus cells have been clearly demonstrated. Again, typical nerve termination cells which appear to be sensory in character, have not been found. The ampullæ of Lorenzini may be sensory, secretory, both or neither. The main problem then of the present investigation is to find out which of these hypotheses is the correct one. First to see what results might be had by using the experimental method, and then to see if the histological structure of the ampullæ supports those results.

The Gross Anatomy of an Ampulla.

The external openings of the ampullæ are usually single, and nearly circular, although there are cases found where the openings are double, when the two ducts connect with one ampulla. When a double opening occurs the two openings are in the form of semi-circles, so that the size and contour of the double openings is much the same as that of a single one. In the case of a single opening, the main or primary duct extends back to the ampulla itself, but when there are two openings the double ducts are parallel and closely approximate. (Fig. 16-A). Never did I find a case where there was a double duct from one ampulla in which the two tubes ran in different directions to the surface as Forsell (98) mentions.

Each duct leads directly downwards from the opening for a short distance, and then widens out quickly to about twice the diameter of the terminal portion. (Fig. 15-A). This is true no matter whether the main duct is single or double in character. The length of the enlarged ducts varies from six to thirty millimeters. They are longest in the posterior ampullæ of the two dorsal groups, and in the posterior ampullæ of the two lateral groups, ventral and anterior to the mouth.

As the duct approaches the ampullary end the main duct is constricted to about three-fourths its former diameter (Fig. 15-B), and the duct divides into two secondary tubules. These immediately subdivide into two or more ducts of tertiary order on the ends of which are the pockets or alveoli (Fig. 15C), these varying in number on the various tertiary tubes. Some of the alveoli, however, lead directly into the main duct. A careful study of

those cases in which there are double ducts leading to the surface, as described above, shows that these are to be regarded as greatly elongated secondary ducts (Fig. 16-A), as there does not seem to be any evidence of a branching which would be called tertiary if these ducts were regarded as primary. The alveoli are not on the same level, so that a section through any one plane would not show all of them. This explains why so many of the writers have stated their numbers to be less than is actually the case. There are partitions between the alveoli, so that the lumen of the ampulla is divided into as many compartments as there are alveoli. In about a dozen ampullæ the average number of alveoli was twenty-two, the range of those counted being between eighteen and thirty-two, the majority being from eighteen to twenty-six. The alveoli are elongate in the direction of their major axis, but circular in outline, with their greatest width near the middle. They differ essentially from those described by Boll (68) and Peabody (97) in that Acanthias has no "centrum" cap to which the partitions run. Here the partitions merely separate the alveoli from one another, terminating at the distal end as sharp ridges. The average diameter of the ampullæ in Acanthias is greater than that of six tenths of a millimeter recorded by Peabody for Galeus, as the approximate diameter of those in an adult female about four feet long was; opening one millimeter, duct two millimeters, and ampulla one and six tenths millimeters. The number of ampullary alveoli is also greater in Acanthias than in Galeus or Mustelus.

Do the Ampullæ of Lorenzini Respond to Outside Stimuli?

The experiments carried on by Parker (1910) in his paper on the influence of the eyes, ears, and other allied sense organs on the movements of the dogfish *Mustelus canis,* were repeated in so far as they related to the ampullæ of Lorenzini in *Acanthias vulgaris.* The experiments were carried on in a floating car six feet square and four feet deep. The sides and bottom of the car were covered with wire netting. The fish were mostly adults which had been caught with a hook, and carefully brought to the car in a barrel of sea water. All of the fish in the car which were experimented on were in good condition, and seemed to be fully normal. They

soon got used to their cramped quarters, and seemed in every way to be fit subjects for experimentation.

Several of the fish were experimented on with more or less success. The first thing tried was to cut the nerves leading to the ampullæ, and to observe the fish swimming around in the car to see whether or not their behavior differed from the other uninjured occupants of the car in any way. Of a number of fish treated in this way, including a number of young "garters" as well as adults, not one of them, as far as could be observed, suffered any inconvenience from the loss of the use of these organs, or any deviation from the behavior of other normal and unhurt fish in the car. In fact, the fish which had had the nerves that lead to the ampullæ cut, could not be distinguished from those that were normal, as they swam about in the car.

Following this, a variation of the same experiment was tried. The fishermen in the vicinity of Casco Bay, Maine, have been bothered so greatly in their fishing by the dogfish, that the custom has prevailed of mutilating the fish when caught so there will be no chance of their ever biting a hook again. These fisherman vouch for the fact that if the tip of the nose be cut off, and the fish be put back into the water, it is unable to sink and flounders around on the surface. A number of experiments were performed to see if there was any basis for this statement, and if it had any relation to the loss of the ampullæ which were in that region, but with negative results. The noses were cut so that all or part of the ampullæ were removed, and in some cases even the brain was exposed, but the fish seemed to be able to sink at will, and behaved in this respect as a normal individual. There seems to be no truth in the statement that a dogfish is unable to sink beneath the surface when the ampullæ are removed, or even when the entire tip of the nose is cut away. The explanation of the fishermen's statement lies in the fact that a dogfish when brought into the air immediately begins to swallow air in gulps so that the intestines are filled. Then when thrown into the water the air inside keeps them at the surface whether or not the tip of the nose is cut away. All operations on the fish were carried on under water so that there was no chance for them to take in air. The ampullæ of a single side, both dorsal

and ventral, were removed, but the actions of these fish could not be observed to differ appreciably from the controls. The openings of the ducts were also covered with paint so that stimulus from the outside might be prevented, but without result.

Finally it was decided that the response, if any, needed more delicate methods to make itself evident. Following Parker, a patch of skin about two centimeters in diameter was dissected away immediately over a bunch of ampullæ, thus removing any possibility of a response to a stimulus from the sensory nerve endings in the skin. The fish treated was an adult female, the most active and well, as also the largest. After a half hours rest given in order that the fish might be fully recovered from the shock of the operation, various stimuli were applied to the ends of the cut canals which had been exposed. A thin delicate needle point was applied to the canal coming from one ampulla, but no reaction could be observed. Possibly there was a reaction, but it was so small that it could not be detected. Then the blunt end of a dissecting needle handle was very carefully applied to a fresh spot, so that there was no danger of touching the wounded edges of the cut skin, at the same time trying to touch the fish with the hands as little as possible, when it was on the surface of the water at the top of the car. This proved to be a difficult undertaking, as the fish was very active, and showed a distinct preference for the bottom of the car. In order that the results could be relied upon, it was thought best not to try to hold the fish at the top of the water, but after a little practice the fish could be made to stand still long enough for its reactions to be seen. Later it was noticed that the reactions seemed to be the same whether or not the fish was held lightly in the hands while the stimulus was applied.

The normal respiration of the fish was from 42 to 48 spiracular closures per minute. A number of stimulations were made, using the blunt point and watching the spiracular valve for an indication of a response. So far as could be noticed this valve did not change its rate of movement, nor was the rate of respiration retarded as Parker states. Upon turning the fish slightly so that the mouth could be observed, a very distinct reaction was noticed. During the normal respirations the mouth is opened, and some of

the water is taken in there, as well as through the spiracle. The distance the mouth is opened in the fish under observation was normally about one-half inch at each inspiration. The instant a light pressure was applied to the ends of the cut canals with the blunt point, the mouth immediately closed, but the respiration continued without a halt, all of the water being taken in through the spiracle. The pressure, if applied less than ten seconds caused the mouth to be closed all during the time that the stimulus was applied. If, however, the pressure was continued for longer than ten seconds, the mouth would open after 7 to 8 complete inspirations through the spiracle, and the water would again be taken in through both places, although the mouth never opened to its normal extent while the stimulus was being applied. If the pressure then be slightly increased the mouth would close entirely again for about ten seconds, until it seemed that the fish "got used" to the stimulus. In every case when pressure was relieved the fish gave a distinct gulp with its mouth, giving the observer an impression that it was greatly relieved at being rid of the stimulus. All of these responses to pressure entirely disappeared upon cutting the nerves supplying the ampullæ. All of the foregoing shows beyond a doubt that these organs were sensitive to the stimulus of pressure caused by the application of the blunt point to the cut canals of the ampullæ. These experiments confirm Parker in that the ampullæ of Lorenzini respond to pressure, but in no case did I get an inhibition of the respiratory movements which could be noticed, as did Parker in his experiments. The response was easily seen, and occurred in other dogfish in the same manner upon later experimentation. These results would indicate that whether or not there be a secretory function, these organs most certainly have a sensory function.

The Histology of the Duct and Ampulla.

The walls of the duct are lined with a single thin layer of squamous epithelium, with a thin layer of fibrous connective tissue on the outside. (Fig. 5-C). With iron alum hæmatoxylin the nucleus and cytoplasm of these cells stain very darkly, even when extracted so that the nuclei of the other epithelium in the ampullæ are clear. This makes it somewhat hard at first to see the nuclei in the wall of the duct, but careful extraction for that point alone will

give good results. The cytoplasm of the cell stains very deeply and seems to be somewhat striated in character. (Fig. 6). Near the ampullary end of the duct there are protoplasmic projections extending out from those squamous cells into the lumen. (Figs. 5-G, and 6-B). These were at first thought to be artifacts, and every possible precaution was taken to prevent any artificial distortion of the cells, but the processes are real and can be seen in all well fixed preparations such as those fixed in Flemming's fluid. These processes arise just above the nucleus, and project a short distance into the lumen. The protoplasm immediately below them is vacuolated, and I am sure that these processes are not cilia. (Fig. 6-C). The number of processes on each cell varies and, as a rule, the farther away from the ampullary end, the fewer the number of processes, until finally there is only a convex contour to the cell, and then a normal squamous epithelial cell with no traces of any projections. (Fig. 5-H). Material which had been fixed in Flemming's fluid was used for studying these processes. It was stained in iron alum hæmatoxylin which was extracted except for the chromatin in the nucleus and then a sharp counterstain with acid fuchsin, much more than would be needed for an ordinary counterstain, for these processes are not visible with the ordinary amount of counterstaining. This overstain brings out clearly the vacuolations in the processes, although the rest of the cell is overstained. All kinds of methods were used and numerous stains tried to be sure of these structures, and all showed them to a more or less degree, even those which gave poor preservation. So I think that it is fairly certain that these are real structures and not artifacts. I could get no hint of their function.

These processes continue into the secondary and tertiary tubes, and are on the partitions between the alveoli, but are not found on the epithelium of the alveoli themselves. (Figs. 5-F, 7 and 8).

At the junction of the ducts and the alveoli, the epithelium and the connective tissue continues, the latter showing little change except that it is thicker, a condition continuing over the outer surface of the alveoli. (Fig. 5-B). The epithelium of the alveoli is best seen in longitudinal sections. (Fig. 5). It is thicker than that

of the ducts and is composed of two types of cells. At first sight there are apparently two layers, as described by Peabody (97), but this is, I think, based on misinterpretation of sections, at least as far as the evidence in Acanthias shows. (Fig. 5-D). The two types of cells differ markedly in shape of cells and position of nuclei. These are (1) larger cells with their approximately circular nuclei near the basal membrane of the epithelium, (Fig. 9, A, E, C, and F.) and (2) smaller cells (interstitial cells) with pyriform nuclei which lie near the free surface of the epithelium. (Fig. 9, G, D, and B). It is this stratification of nuclei which conveys the idea of a stratification of the epithelium, but careful observation, especially in rather thick sections has convinced me that both types of cells extend from the basal membrane to the free surface. (Fig. 9, A and B). The cells of the larger type are so large that there are not many in each section which are cut directly through the center so that both basal and distal surfaces are shown, but these are seen in a number of cases in thin sections (Fig. 9-A), and I think that nearly every cell in the epithelium extends from the basal membrane to the free surface of the epithelium.

The protoplasm of the larger cells is vacuolated (Fig. 9-E), and the chromatin in the nucleus forms a rather coarse network (Fig. 9-C), while the protoplasm in the interstitial cells is rather striated in character (Fig. 9-G), and the chromatin in the nucleus forms a finer network with scattered granules, giving these a much darker appearance. (Fig. 9-D). In no case have I found a cuticle lining the free surface of the alveoli next to the lumen, as Forsell (98) has described for Acanthias.

Innervation.

The different groups of organs are supplied by several branches of the lateralis componant of the facial nerve, as indicated on page 134, a single twig containing from five to ten medullated fibres running from the main ramus to each ampulla. These twigs run to the centre of the ampulla into the space between the alveoli. There they lose their sheaths, and each breaks up into fibrillæ. These pass out between the alveoli, and form a network upon their outer and anterior surfaces. (Figs. 10 and 11).

Many methods of impregnation were tried in the attempt to discover the method of termination but all were failures, with the exception of intra vitam staining with methylen blue. This, at best, is uncertain, attacking as it does only certain of the fibres and fibrillæ, and one can never be sure that every portion has taken the stain. Several fairly good impregnations were obtained, and these indicate that the fibrillæ had enlargements in their course (Figs. 10, 11 and 14), and that they sometimes terminated with similar end organs. (Figs. 12 and 13). In every case where exact determination was possible, it was found that these enlargements were upon the bases of the pear-shaped cells of the alveoli and in no case were they found connected with the other cells of the epithelium, nor did the nerves extend on to the walls of the ducts.

These facts seem to favor a sensory function for the ampullæ. There are a number of specialized cells which are in a position to receive stimulation, as the pear shaped cells are in direct connection with the mucus in the ampullæ, and have a connection with branches of the nerve supplying the lateral line organs which are certainly sensory in function. The fact that there are no hair cells does not preclude a sensory function as there are numerous instances in which distinctly sensory nerves are not connected with hair cells. The general agreement is that these ampullæ, and the ear as well, are genetically connected with the lateralis system of organs. Hence the fact that Morrill (97) found sensory cells in the dogfish ear which had no hairs, is of especial interest in this connection. Then again there is no need of continuity between nerve and cell, as Morrill also found in his description of the sensory cells in the ear of Mustelus.

The Functions of the Mucus.

In many of the accounts of these organs the figures show a peculiar striation of the mucus contained in the ampullæ and the ducts leading from them, and some authors have discussed the structure and meaning of this appearance at some length. (Forsell 98). In material taken fresh from the dogfish there is nothing of the sort to be seen, but it always appears in the fixed material, but the character of the striation or fibration varies with the reagent

used. (Figs. 5 and 6-A). These facts lead me to the conclusion that the appearance is really an artifact.

The mucus of the ampullæ is not needed to lubricate the body, as there are numerous goblet cells all over the body for that purpose. Also in the adult fish there is no evidence of a discharge of mucus when alive. The mucus appears when the ampullæ are squeezed, but otherwise it is not seen. That is to say, no more mucus is found on the surface of the body in the region of the ampullæ than at any other point. Apparently there is little loss of mucus from the ampullæ, all that is lost being worn away by friction of the water at the opening of the duct. Therefore the ampullæ need but little mucus to keep the tubes full. If this view be correct it would explain why so little evidence of mucus secretion is found. Treatment with mucicarmin shows very few cells taking the mucus stain. These cells are isolated and are in the same position as the pear-shaped cells, but are somewhat narrower, have smaller nuclei, and have a greater portion of the cell bordering on the lumen. They greatly resemble the pear-shaped cells and in sections stained in the usual way it is impossible to distinguish between the two. I did not succeed in determining whether or not they are innervated. Some of the sections of the ampullæ do not show any of these cells, so it is evident that they are not common. Again it may be said that the blood supply of the ampullæ is very small. This would imply that the secretory function is very limited—merely enough to replace the slight loss, as a large blood supply would be needed for an extended production of mucus.

The ampullæ are situated beneath the skin in the connective tissue, and are connected with the surface of the body by long ducts. It is therefore certain, that if any stimulus is to reach the sensory cells in the pockets, it must either be transmitted through the overlying integument or it travels to them through the mucus. This, then may be the function of the mucus in the ampullæ—to act as a conductor, by means of which stimulation from the outside is to reach the sensory portions of the ampullæ.

Summary and Conclusions

It therefore appears from both experimental results and from histological structure:

A. That the ampullæ of Lorenzini in Acanthias vulgaris are primarily sense organs.

B. That they have a secretory function in so far as it is necessary to keep up the supply of mucus in the ampullæ and their ducts. This need is small, as there is little loss.

C. That they respond to the stimulus of pressure, and from the fact that the ducts radiate in all possible direction—

D. That the pressure may be caused by currents of water impinging on some of the ampullæ harder than others, thus giving the fish a sense of the direction of the source of the stimulus.

E. That also by means of these ampullæ the dogfish may determine by means of pressure, the depth of water in which it is swimming.

F. That it is also possible that these organs will respond to the deeper notes as these would cause a vibratory change of pressure on the ampullæ.

G. That these ampullæ from their innervation and their function are rightly classed as sense organs along with the lateral line system in the Selachians.

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Fig. 5

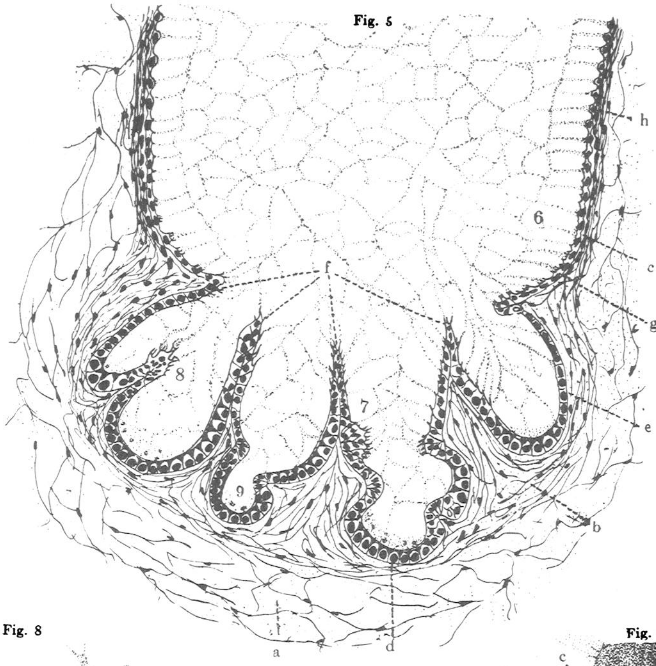

Fig. 8

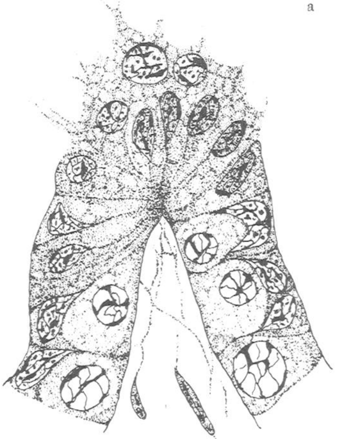

Fig. 6

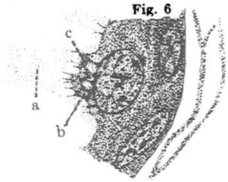

Fig. 7

Fig. 9

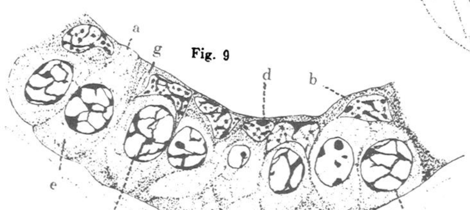

Plate IV

EXPLANATION OF PLATES

Plate IV

Fig. 5. A semi-diagrammatic drawing of a longitudinal section of an ampulla. Flemming's fluid, iron alum hæmatoxylin and eosin. X 200.

Fig. 6. An enlarged portion of the duct showing the protoplasmic processes and the mucus striation. Flemming's fluid, iron alum hæmatoxylin and eosin. X 800.

Fig. 7. A cross section of the protoplasmic processes on the partition between two alveoli. Flemming's fluid, iron alum hæmatoxylin and eosin. X 800.

Fig. 8. A cross section of the protoplasmic processes on the partition between the partition between the alveolus and the duct. Flemming's fluid, iron alum hæmatoxylin and eosin. X 800.

Fig. 9. The epithelium of the alveoli, showing in detail the structure and relationships of the two types of cells present. Flemming's fluid, iron alum hæmatoxylin and eosin. X 800.

The small figures in the lumen of the ampulla shown in Fig. 5 indicate the portions which have been figured in Figs. 6 to 9.

PLATE V

Fig. 10. A thick section through the base of one of the alveoli showing the nerve ramifications over the alveolus. Methylen blue impregnation. X 400.

Fig. 11. A cross section showing the nerve extending laterally after having lost its sheath. Methylen blue impregnation. X 400.

Fig. 12. A thick section showing the method of termination of the nerve fibre on the base of one of the pear shaped cells. Methylen blue. X 950.

Fig. 13. A thick section showing the same kind of termination on a slightly differently shaped cell. This difference in shape and the difference in shape between these cells and the same cells fixed in Flemming's fluid as figured above, may be explained by the fact that the methylen blue process gives poor fixation. X 950.

Fig. 14. A thick section showing two of the pear shaped cells which have a slight enlargement of the nerve fibre at their base, with no termination. X 950.

Figures 6 to 14 are camera drawings.

Fig. 15. A diagram of an ampulla and duct with a single duct.

Fig. 16. A diagram of an ampulla and duct with a double duct.

Fig. 10

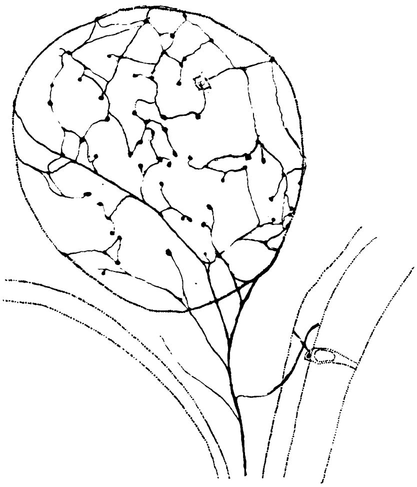

Fig. 12

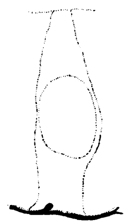

Fig. 13

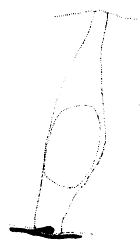

Fig. 14

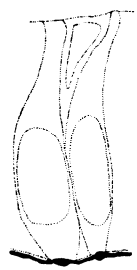

Fig. 11

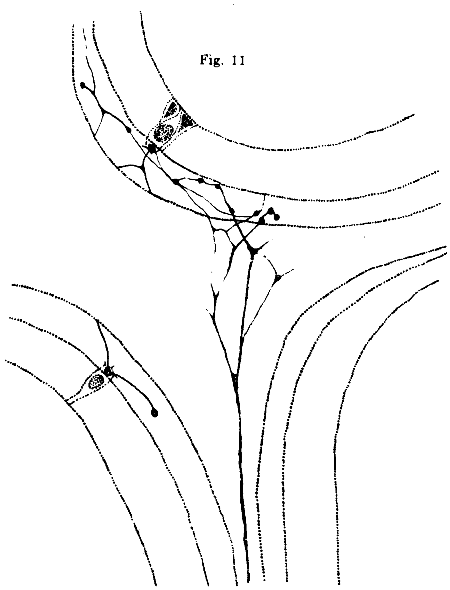

Fig. 15

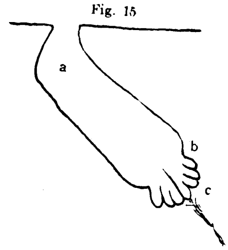

Fig. 16

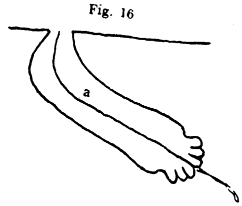

PLATE V